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Chemical reactors of the mammalian gastro-intestinal tract

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Abstract

This study reviews and defines the classes of chemical reactors known in mammalian gastro-intestinal tracts, describing how they differ from the "ideal reactors" of chemical engineering. Three classes of reactors are present in the mammalian guts: batch reactors, plug-flow reactors and continuous-flow, stirred-tank reactors. These are modified from the ideal types in two ways: firstly, the method of transport of reactants through a reactor; secondly, by continual absorption of products throughout the length of the reactor. To avoid confusion with the reactors of chemical engineering, gut reactors are defined as simple and complex types on the basis of their musculature. There are five types of chemical reactor found in mammalian gastro-intestinal tracts – semi-batch reactors (the caecum of caecum fermenters), simple plug-flow reactors (the small intestine), complex plug-flow reactors (the macropodid forestomach), simple continuous-flow, stirred-tank reactors (the unipartite stomach) and complex continuous-flow, stirred-tank reactors (the haustrated colon of colon fermenters). Application of chemical reactor theory to gut function is an important tool in understanding the relationships between morphology, diet chemistry, and digestive processes in mammals.

Key words: Mammals, gastro-intestinal tracts, modified chemical reactors

Introduction

In 1986, Penry and Jumars used chemical reactor theory to describe the processes of digestion in animals, as the ability to process substrates (from the food) in bulk is the basic requirement of any gastro-intestinal tract (Penry and Jumars 1986). Industrial reactors are designed to optimise the return of products from a particular chemical reaction within given 'economic' constraints (Denbigh and Turner 1971). Digestive processes operate under similar economic constraints, resulting in the optimisation of the return of nutrients to an animal from its diet (Sibly 1981; Penry and Jumars 1986; Hume 1989). The reactors of chemical engineering (called ideal reactors in this review) differ in a number of operating features from those found in the mammalian gastro-intestinal tract. There is a need to clarify these differences and to define the characteristics of mammalian gut reactors (Caton 1997).

The application of chemical reactor theory to gastro-intestinal tract function has provided a means of understanding the complexity of the physiological relationships between an animal and its food (Hume 1989). Application of reactor theory also permits an integrated approach to this problem through the development of mathematical models of digestive processes (Penry and Jumars 1987; Alexander 1991; Martinez Del Rio et al. 1994). Quantifiable predictions of digestive function can then be made with reactor mod-

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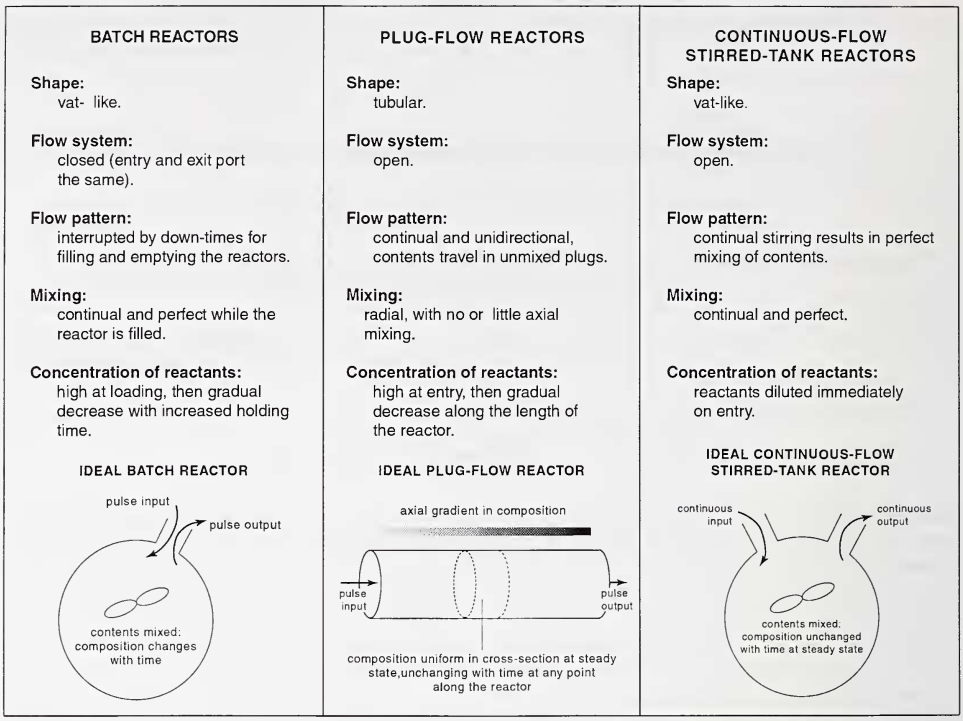

Fig. 1. The three types of idea reactors that have analogues in animal digestive systems (after STEVENS and HUME 1995 and CATON 1997). Batch reactors, with a single entry-exit port best describe gut compartments that process digesta in discrete batches, e. g. the mammalian caecum. The vertebrate mid gut functions as a tubular plug flow reactor. Continuous-flow, stirred-tank reactors are vat reactors similar to those seen in the compartments of the ruminant forestomach.

els, using physiological parameters from living animals to predict optimal reactor types and thus the optimal morphology and physiology for processing specific diets (HUME 1989; MARTINEZ DEL RIO et al. 1994; CATON 1997).

Chemical engineers use three types of ideal reactor when designing plants for the bulk processing of chemicals – batch reactors, plug-flow reactors and continuous-flow, stirred-tank reactors. Each of these types has performance characteristics that allow optimisation of returns from specific chemical reaction systems, a factor of considerable importance when modeling gut function (PENRY and JUMARS 1986; HUME 1989; MARTINEZ DEL RIO et al. 1994). Functional characteristics, such as flow patterns (induding mixing of contents), retention times and performance (reaction rate), are important in determining the suitability of a particular reactor for a given set of reactions (DENBIGH and TURNER 1971). Before describing gastro-intestinal reactors it is necessary to define the characteristics of ideal reactors, as these provide the basis for understanding the function of the modified reactors of the mammalian gastro-intestinal tract.

Characteristics of Ideal Reactors

Batch reactors are used for processing small quantities of reactants in discrete volumes or batches. All the reactants are introduced into the chamber at the same time (pulse input), and subsequently all products with any unreacted fractions are removed as a pulse output

(Denbigh and Turner 1971) (Fig. 1). In batch reactors reaction periods alternate with "down-time" periods during which the reactor is emptied and then loaded again (Denbigh and Turner 1971). Batch reactors are closed systems with single entry-exit ports (Fig. 1), thus there is no flow in or out during the operating period (Karasov and Diamond 1988; Penry 1993). During the operating or holding time, the contents of an ideal batch reactor are perfectly mixed (homogeneous) and changes in composition occur only with respect to time (Penry and Jumars 1986, 1987). The functioning of the reactor continues either for the time needed to reach thermodynamic equilibrium, or until the reaction is stopped (Denbigh and Turner 1971). Holding time is the most important operating variable with a batch reactor, as the longer the reactants remain in the reactor the greater the extent of their conversion (Penry and Jumars 1986). In these closed systems reaction rates are high initially, gradually slowing as the residence time increases and the reactants are depleted. Holding time in a batch reactor equals both residence time and mean residence time, as there is no throughput flow (Denbigh and Turner 1971). Both holding time and down time are important when considering the efficiency of a batch reactor (Martinez Del Rio et al. 1994). The interruption of the down times effectively limits reactor performance, so that overall production rates are generally low (Denbigh and Turner 1971; Hume 1989). The effect of reactor down time can be compensated for by increasing the volume of the reactor (Hume 1989; Martinez Del Rio et al. 1994), or by the continuous removal of the products as occurs in a semi-batch reactor (Penry 1993).

Plug-flow reactors are usually tubular in shape (Fig. 1), and were defined by Denbigh and Turner (1971) as "... any continuously operating reactor in which there is a steady movement of one or all reactants in a chosen spatial direction (reactants entering at one end of the system and leaving at the other) and in which no attempt is made to induce mixing between the elements of the fluid at different points along the direction of flow." For any cross sectional area of a plug-flow reactor, mass flow rate and fluid properties are uniform. All elements of the fluid (which may be described as travelling in small, self-contained envelopes) spend equal time passing through the reactor, and undergo the same sequence of pressure, temperature and concentration changes. Characteristically, reactants and products do not diffuse between these plugs during their passage through the reactor (Denbigh and Turner 1971). As a result, the reaction must occur to the same extent in each element of the fluid. Plug-flow reactors are thus regarded as miniature batch reactor systems travelling through a tubular reactor (Denbigh and Turner 1971).

By definition, any plug-flow reactor is an open system (Fig. 1), characterised by the uni-directional flow of material between separate entrance and exit ports (Denbigh and Turner 1971; Hume 1989). With this pattern of flow there is no accumulation of reactants within the tubular vessel, and no dilution of reactants on entry to the reactor (Denbigh and Turner 1971). Flow within the reactor is laminar, with negligible diffusion relative to bulk flow resulting in little or no axial mixing (Denbigh and Turner 1971; Martinez Del Rio et al. 1994). For steady state operation in a plug-flow reactor the gradient in the concentration of reactants and products remains constant throughout the length of the reactor (Martinez Del Rio et al. 1994). Increasing the length enhances the performance of plug-flow reactors, with a resultant increase in the degree of radial mixing (Martinez Del Rio et al. 1994).

Reaction rates and the concentration of reactants are highest at the entrance, then gradually decline along the length of a plug-flow reactor (Hume 1989; Martinez Del Rio et al. 1994). Performance of a plug-flow reactor is measured by the fraction of reactant converted to product (measured at the exit), thus through-put time is important in assessing performance (Martinez Del Rio et al. 1994). Residence time distribution, mean residence time and through-put time of material in the effluent fluid are all equal in a plug-flow reactor, and there is no spread of residence times (Denbigh and Turner 1971). Performance is generally high in this type of reactor as function is continuous,

with no down time as in a batch reactor (HUME 1989; MARTINEZ DEL RIO et al. 1994). In industry, plug-flow reactors are used extensively for catalytic reactions (DENBIGH and TURNER 1971).

Continuous-flow, stirred-tank reactors are tanks or vats with well-mixed contents, into which "... there is a continuous flow of reacting material, and from which the (partially) reacted material passes continually" (DENBIGH and TURNER 1971). Continuous-flow, stirred-tank reactors are open systems with separate entry and exit ports (Fig. 1). The characteristics of continuous-flow, stirred-tank reactors include dilution of reactants immediately on entry by contents remaining from previous runs, the constant flow of material through the reactor, and the complete mixing of the contents (DENBIGH and TURNER 1971). At steady state the composition of the contents of the reactor is spatially homogenous with respect to time (PENRY and JUMARS 1986). Under these steady state conditions there is no dead space within the reactor and the effluent stream has the same composition as its contents. Increasing the viscosity of the reactants impedes mixing and reduces performance (DENBIGH and TURNER 1971). Structural baffles built into the wall of a continuous-flow, stirred-tank reactor are used to assist mixing of reactants (DENBIGH and TURNER 1971).

Residence times of molecules in a continuous-flow, stirred-tank reactor will vary because of the continual mixing. In the ideal reactor with perfect mixing, residence time, mean residence time and throughput time would all be equal (PENRY and JUMARS 1987). The broader the range of residence times and the faster the flow through the reactor the lower the performance (DENBIGH and TURNER 1971; HUME 1989). By-pass loss is another important consideration with any continuous-flow, stirred-tank reactor, as there is a significant probability that a given molecule entering the system will pass directly into the outflow. While by-pass loss is the result of stirring, the loss would be greater without mixing due to bulk streaming (DENBIGH and TURNER 1971). By-pass loss can be overcome by having several continuous-flow, stirred-tank reactors in series, thus achieving a higher overall rate of conversion (DENBIGH and TURNER 1971).

Comparison of Ideal Reactor Function

Reaction rates in continuous-flow, stirred-tank reactors tend to be lower than in either batch reactors or plug-flow reactors, and continuous-flow, stirred-tank reactors are best suited to comparatively slow liquid-phase reactions (DENBIGH and TURNER 1971). Greater volumes of reactants must be processed if a continuous-flow, stirred-tank reactor is to give results equivalent to those of the other two (DENBIGH and TURNER 1971). Overall yield can be raised considerably if several continuous-flow, stirred-tank reactors are used in series (DENBIGH and TURNER 1971). The advantage of continuous-flow, stirred-tank reactors is that the continual mixing of incoming reactants with the reaction products makes it possible to operate these reactors continually at the lowest point of the reaction rate (DENBIGH and TURNER 1971). It is found that higher reaction rates are achieved in continuous-flow, stirred-tank reactors with fermentation reactions than with catalytic reactions (DENBIGH and TURNER 1971).

Gastro-intestinal Reactors

The characteristics of the three dasses of ideal chemical reactors are compared in figure 1. Analogues of the three classes of chemical reactor are found in the gastro-intestinal tracts of mammals, in which each type performs a different set of digestive functions (Figs. 2–4). Chemical processing of food macromolecules during digestion involves their hydrolysis to smaller component molecules in the presence of a range of catalysts (enzymes). Digestive

processes can be divided into two broad groups on the basis of the source of these enzymes (Stevens and Hume 1995). Catalytic reactions involve endogenous enzymes that are manufactured and secreted by glands of the digestive system. High-quality components of the diet (proteins, lipids, simple sugars and starches) can be digested by endogenous enzymes (Stevens and Hume 1995). Fermentation tends to be slower and is controlled by exogenous enzymes produced by symbiotic micro-organisms living within the gut. Structural polysaccharides from plant material, which cannot be processed by catalysis, are digested by these micro-organisms (Stevens and Hume 1995). Catalytic and fermentation reactions have different processing requirements and produce different end-products (Denbigh and Turner 1971; Penry and Jumars 1987; Hume 1989; Alexander 1991; Martinez Del Rio et al. 1994). A priori, it must follow that:

(1) A reactor cannot perform catalytic and fermentation functions at the same time.
(2) Different types of chemical reactor will be more efficient and thus better suited for different types of organic compounds in the diet.

These factors have important implications for the development of models of gut function in mammals.

Gastro-intestinal reactors differ from ideal reactors in two ways. Firstly, the 'pump' moving the contents through a gut reactor is intrinsic or part of the wall, unlike ideal reactors in which the pump is extrinsic. Movement of gut contents is the result of activity of cells in the two layers of the external muscle coat, or tunica muscularis, of the wall. The movements produced by the muscle cells in these layers is complex, resulting in mixing and in the overall transport of digesta from mouth to anus. The control of this muscular activity is also complex, and dependent upon neural, hormonal and intra-mural factors triggered by the physical and chemical nature of the digesta.

The second difference is the method of removal of the products of the reactions, or nutrients, as they are continually absorbed across the lining of the lumen, the tunica mucosa, into the bloodstream. Removal of products in blood flowing through the mucosal capillaries produces concentration gradients that result in an increased rate of nutrient removal from the lumen of the reactor. This absorption process is important as it facilitates digestion reactions, which are slowed or stopped by increasing concentrations of products in the reactor (Denbigh and Turner 1971). Absorption is a general function of the mucosa of the entire gastro-intestinal tract.

The aims of this review are to define the types of reactors found in mammalian gastro-intestinal tracts, and to describe how they differ from the ideal reactors of chemical engineering. These definitions are based primarily on the results of dissections of mammalian gastro-intestinal tracts, as well as the known physiology of individual gastro-intestinal compartments in mammals, including the results of digesta transit studies (Warner 1981; Stevens and Hume 1995; Caton et al. 1996; Caton 1997).

Materials and method

Gastro-intestinal tracts of a wide range of mammals have been dissected over a period of years; in particular primates (lemurs, monkeys, apes), but also marsupials (both carnivores and herbivores), ruminants (domestic and wild), rodents and lagomorphs. The data collected included descriptions of the gross morphology of the gastro-intestinal tract, with photographs and drawings, and details of the musculature of individual compartment, including the position of the sphincters at compartmental junctions. The length and calibre of individual compartments were measured after careful removal of the mesenteries to avoid stretching the tissues.

Table 1. Comparison of the morphology of gastro-intestinal compartments of mammals.

Compartment	Simple Morphology	Complex Morphology
Stomach	Unipartite; globular to pyriform. Regions – fundus, body, pyloric segment. Mucosal glands secrete mucus, hydrochlorid acid, pepsin. Tunica muscularis – three layers of muscle cells, outer longitudinal, inner circular separated by an oblique layer	Pluripartite; shape variable Regions – forestomach and hindstomach which may be subdivided into smaller compartments. Mucosal glands secrete mucus (forestomach); hydrochloric acid, pepsin and mucus (hindstomach). Tunica muscularis complex – three layers of muscle cells, outer longitudinal, inner circular separated by an oblique layer; longitudinal layer may be divided into 2 discrete bands (taeniae).
Pyloro-duodenal junction – annular pyloric sphincter encircles the lumen; formed by a thickening of the circular muscle coat.		
Small intestine	Elongated tube, relatively uniform calibre; length variable. Regions – duodenum, jejuno-ileum. Accessory glands secrete into duodenum; tubular glands in the mucosa secrete mucus and enzymes. Tunica muscularis – outer longitudinal layer, inner circular layer.	No complex morphology.
Ileo-caecal or ileo-colic junction – annular sphincter encicles the lumen of the terminal ileum; formed by thickening of the circular muscle coat.		
Caecum	Elongate or bag-like diverticulum; variable length. Tubular mucosal glands secrete mucus. Tunica muscularis – outer longitudinal layer, inner circular layer.	Elongate or bag-like diverticulum; variable length. Tubular mucosal glands secrete mucus. Tunica muscularis – outer longitudinal layer, inner circular layer; longitudinal layer divided into 2–4 discrete bands (taeniae)
Caeco-colic junction – annular sphincter encircling the lumen may separate these hindgut compartments; formed by thickening of the circular muscle coat.		
Colon	Elongated tube, relatively uniform calibre; length variable. Regions – proximal colon, distal colon and rectum. Tubular glands in the mucosa secrete mucus. Tunica muscularis – outer longitudinal layer, inner circular layer.	Elongated tube, calibre variable especially of proximal colon; length variable. Regions – proximal colon, distal colon and rectum. Tubular glands in the mucosa secrete mucus and enzymes. Tunica muscularis – outer longitudinal layer, inner circular layer; longitudinal layer divided into 2–4 discrete bands (taeniae)

Results

The results of the study of the morphology of the compartments of the mammalian gastro-intestinal tract are summarized in table 1. The division of compartmental morphology into simple and complex is a reflection of the function of a particular compartment. In general, the chemical functions of compartments with simple morphology are digestion by endogenous enzymes and absorption. Compartments with complex morphologies are fermentation chambers containing micro-organisms capable of digesting non-starch polysaccharides from plant cell walls and insect exoskeletons. Mammals with guts adapted to processing non-starch polysaccharides generally have a single fermentation chamber in their gastro-intestinal tracts. These compartments are easily recognized by their greater capacity and specialized musculature (Tab. 1). The patterns of mammalian gastro-intestinal morphology characteristic of different digestive patterns are outlined in table 2.

Table 2. Patterns of mammalian gastro-intestinal morphology associated with different digestive patterns.

Digestive Pattern	Gastro-intestinal Compartment Morphology			
	stomach	small intestine	caecum	colon
Carnivore	simple	simple	small – simple, or vestigial	simple
Insectivore	simple	simple	simple; size variable	simple
Herbivores				
1. forestomach fermenters	complex forestomach; simple hindstomach	simple	simple; size variable	simple
2. caecum fermenters	simple	simple	enlarged; simple or complex morphology	simple
3. colon fermenters	simple	simple	variable size; simple or complex morphology	proximal colon capacious and complex

Discussion

Compartmentalisation of the gastro-intestinal tract

Unlike most industrial reactors, mammal gastro-intestinal tracts are multi-reaction systems involving parallel or sequential reactions (Petersen 1965). This presents certain design problems or constraints (Martinez Del Rio et al. 1994) which are largely overcome through increasing the total length of the gastro-intestinal tract and the division of the tract into morphologically and functionally distinct compartments.

Compartmentalisation of the gastro-intestinal tract separates catalytic and fermentation reactions. Functional separation also occurs at the molecular level as the result of enzyme specificity (Petersen 1965). This functional separation also includes absorption of the products of these reactions (nutrients) via different routes (Karasov and Diamond 1988; Stevens and Hume 1995). The chemical composition of an animal's diet dictates the type of digestive reaction required. This in turn dictates the type of reactor found in the gastro-intestinal tract. The optimal reactor for catalytic reactions is a plug-flow reactor, for fermentation reactions a continuous-flow, stirred-tank reactor. Batch reactors can be

used for either type of reaction, but not at the same time (DENBIGH and TURNER 1971; CATON 1997). This separation of catalytic and fermentation reactions in the gastro-intestinal tract is the result of differences in operating requirements for the three classes of chemical reactors (Tab. 1). Separation of catalytic and fermentation reactions has the additional advantage of protecting symbiotic micro-organisms from the action of endogenous enzymes.

The optimal reactor types for processing a given diet are dependent upon the reactants and the reaction conditions, as the performance of reactors varies considerably (DENBIGH and TURNER 1971; MARTINEZ DEL RIO et al. 1994). Digesta passage studies based on inert markers, the equivalents of the tracer experiments of chemical engineering, are used to measure gut reactor performance (HUME 1989; MARTINEZ DEL RIO et al. 1994). In batch reactors conversion or performance is a function of holding time and down time (time taken for loading and emptying the reactor) (MARTINEZ DEL RIO et al. 1994). Down time is eliminated by continuous flow of reactants through both batch reactors and continuous-flow, stirred-tank reactors. The dilution of reactants immediately on entry into a continuous-flow, stirred-tank reactor increases the time required for conversion of a similar amount of reactants in a continuous-flow, stirred-tank reactor than in a plug-flow reactor. Batch reactors also operate at higher levels of reactant concentrations than continuous-flow, stirred-tank reactors for the same reactor-feed conditions, at least initially. However, the ability of continuous-flow, stirred-tank reactors to operate continuously at lower concentrations is an important feature in their application, as the reaction rate is the same throughout the reactor due to mixing (DENBIGH and TURNER 1971; MARTINEZ DEL RIO et al. 1994). With highly digestible dietary components, plug-flow reactors out-perform both batch reactors and continuous-flow, stirred-tank reactors achieving the same extent of conversion in less time (DENBIGH and TURNER 1971). The combination of different reactors found in mammalian gastro-intestinal tracts gives them flexibility to process a diverse range of dietary materials (PENRY and JUMARS 1986; ALEXANDER 1991).

Mammals with their long, complicated gastro-intestinal tracts provide examples of the modification of the basic (ideal) reactor types. These modifications reflect different digestive patterns (HUME 1989; CATON 1997). Herbivores and omnivores, which eat large quantities of structural polysaccharides, rely on fermentation to a greater extent than carnivores (STEVENS and HUME 1995). Their complex gastro-intestinal tracts separate the catalytic processing of high-quality dietary components from the fermentation of structural polysaccharides. Chemical reactor models provide the conceptual and mathematical basis for making comparisons of compartmental function and morphology (PENRY and JUMARS 1986; CATON 1997).

Characteristics of gastro-intestinal reactors

The chemical reactors found in mammalian gastro-intestinal tracts are modified from the ideal types as the walls of the compartments function as both conduits and pumps, unlike industrial reactors in which these two functions are separate (DENBIGH and TURNER 1971; WEEMS 1987). In industrial reactors products are removed at precisely determined intervals along the reactor or at the exit port (DENBIGH and TURNER 1971). In the gastro-intestinal tract, however, there is continual removal of reaction products by absorption through the wall, while undigested residues pass either to the next reactor or are eliminated to the environment (WEEMS 1987; STEVENS and HUME 1995).

These modified reactors are associated with the different functions of a particular compartment of the tract (usually catalysis versus fermentation) that reflect evolutionary changes that enable mammals to exploit new dietary niches, e. g. from insectivory to herbivory (CATON 1997). These changes involved alterations to existing structures enabling them to perform new tasks, rather than adding new compartments to the gastro-intestinal

tract. The distinctions between the classes of gut reactors are often not as clear as those seen in the ideal three types, with the result that the modified reactors are hybrids (Hume 1989). Martinez Del Rio et al. (1994) considered that the three classes of ideal chemical reactor are points on a continuum, noting that: "A long series of CSTRs [continuous-flow stirred-tank reactors] behaves like a PFR [plug-flow reactor] and the behaviour of a plug-flow reactor with intense recycling resembles that of a CSTR". Denbigh and Turner (1971) made a similar point when they wrote that the radial mixing of the contents in plug-flow reactors resulted in their functioning as a series of small batch reactors. Chemical reactor theory provides a mathematical basis for comparing the functions of the gut reactors with the performances of the ideal types (Penry and Jumars 1987).

The modified plug-flow reactor of the macropodid forestomach was the first gut reactor recognised as differing from the ideal (Dellow and Hume 1982) (Tab. 3). Penry (1993) considered the mammalian caecum to be a semi-batch reactor, as there is continual absorption of products from the lumen and continual filling, but discontinuous emptying. Comparison of morphology, function, and digesta flow patterns of the various gastro-intestinal tract compartments with the characteristics of ideal chemical reactors indicates that gut reactors can be divided into simple and complex types (Tabs. 1 and 4). The musculature is of particular importance in defining gut reactor type (Caton 1997).

Semi-batch reactors are the only form of batch reactor found in the mammalian gastro-intestinal tract (Penry 1993). They are usually sites of fermentation containing large populations of micro-organisms (Stevens and Hume 1995). The ruminant forestomach has the morphological and functional characteristics of a semi-batch reactor (Tab. 3). The caecum is also a semi-batch reactor, enabling mammals to process plant structural polysaccharides, exudates and chitin from arthropod exoskeletons (Hume and Sakaguchi 1991; Caton et al. 1996; Caton 1997) (Fig. 2). Continual removal of products results in increased reaction rates in semi-batch reactors (Penry 1993). The flow of reactants between

Table 3. Terms used by various authors in descriptions of the modified chemical reactors of the mammalian gastro-intestinal tract compared with those discussed in this study.

Batch reactors	Plug-flow reactors	Continuous-flow, stirred-tank Reactors	Source
IDEAL caecum	IDEAL small intestine	IDEAL simple stomachs, ruminant forestomach	Penry and Jumars (1987)
IDEAL possibly the caecum	IDEAL small intestine	IDEAL simple stomachs, ruminant forestomach	Hume (1989)
	MODIFIED macropodid forestomach		
	IDEAL small intestine	IDEAL ruminant forestomach; haustrated proximal colon	Alexander (1994)
SEMI-BR caecum			Penry (1993)
SEMI-BR caecum	SIMPLE small intestine	SIMPLE reticulum of ruminants	This Study
	COMPLEX macropodid forestomach	COMPLEX haustrated proximal colon with the caecum	

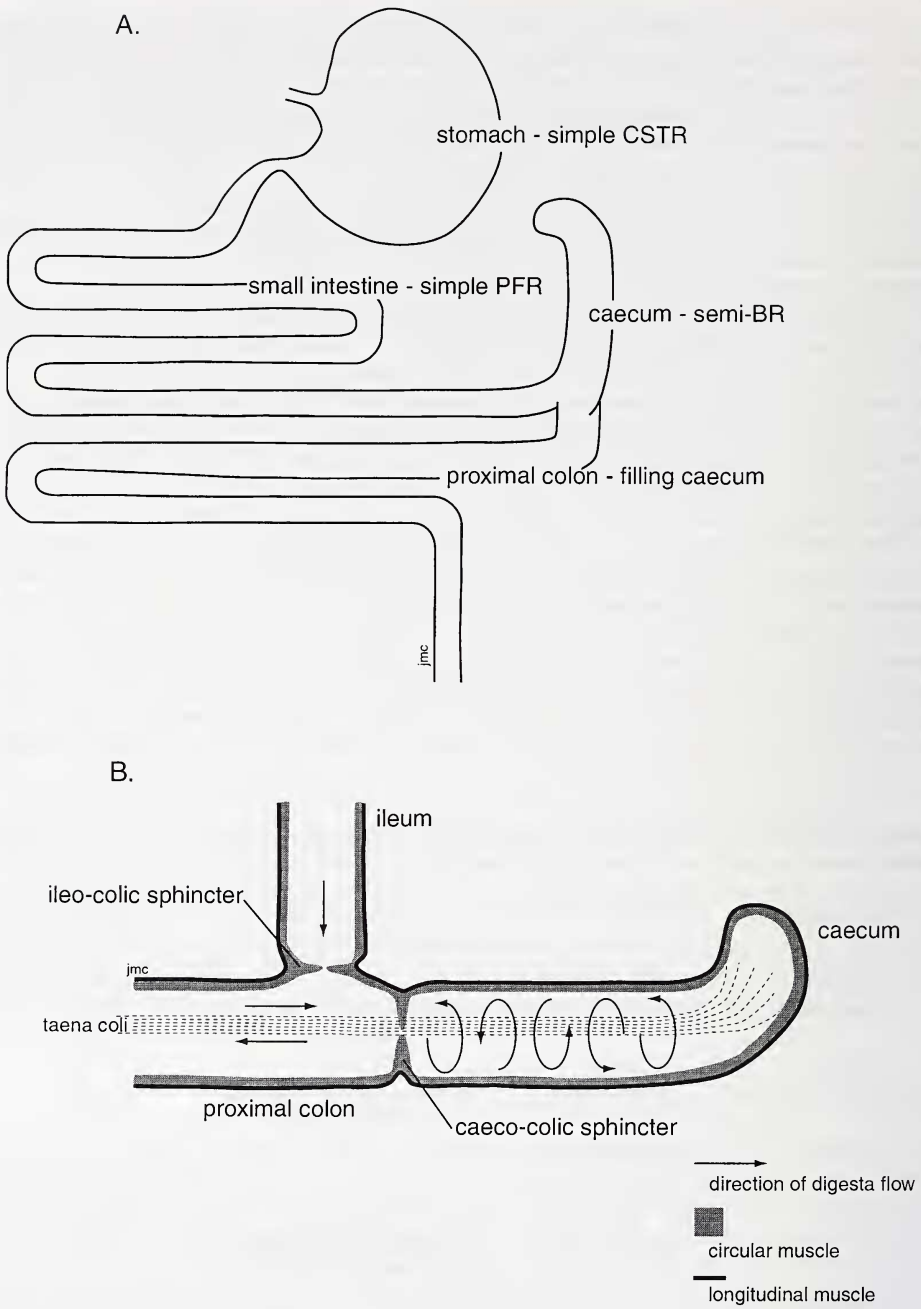

Fig. 2. The gastro-intestinal tract (A) of the common marmoset (*Callithrix jacchus*), with details of the caecum (B), which functions as a semi-batch reactor. The caeco-colic sphincter would remain closed during fermentation of batches of digesta. The contents of the caecum are mixed by contractions of the circular muscle layer of the tunica muscularis and by contraction of fibres of the single taenia coli. Abbreviations: CSTR, continuous-flow, stirred-tank reactor; PFR, plug flow reactor; semi-BR, semi-batch reactor.

Table 4. Comparison of the functional characteristics of the modified reactors of the mammalian gastro-intestinal tract. Calculations of surface area-to-volume ratios based on data from CHIVERS and HLADIK (1980).

Reactor Characteristics	Semi-batch	Plug-flow		Continuous-flow, stirred-tank	
		simple	complex	simple	complex
Shape	vat-like	tubular (smooth-walled)	tubular and haustrated	vat-like	tubular and haustrated
Flow system	closed	open	open	open	open
Flow pattern	not interrupted by down-times as continuous absorption of products	continuous and unidirectional	continuous and unidirectional	continual stirring with perfect mixing of contents	contents are moved back and forth by alternating peristalsis and antiperistalsis.
Mixing	continual and perfect while the reactor is filled	radial with no axial mixing	radial in individual haustra, with localised axial mixing in the individual haustra.	continual and perfect	contents mixing by alternating peristalsis and antiperistalsis, also by localised mixing movements of individual haustra
Concentration of reactants	high at loading, then gradual decrease with increased holding-time	higher at the reactor entry than at the exit	higher at the reactor entry than at the exit	reactants diluted immediately on entry to the reactor	reactants diluted immediately on entry to the reactor
Absorption	continual absorption of products through the walls	continual absorption of products throughout the reactor	continual absorption of products throughout the reactor	continual absorption of products throughout the reactor	continual absorption of products throughout the reactor
Digestive process	fermentation of soluble polysaccharides, e. g. the marmoset caecum	catalytic digestion, e. g. the mammalian small intestine	fermentation of plant cell walls, e. g. macropodid forestomach	1. catalytic digestion, e. g. the unipartite mammalian stomach 2. fermentation of plant cell walls, e. g. ruminant reticulum	fermentation of structural polysaccharides, e. g. catarrhine, pig and equine proximal colons

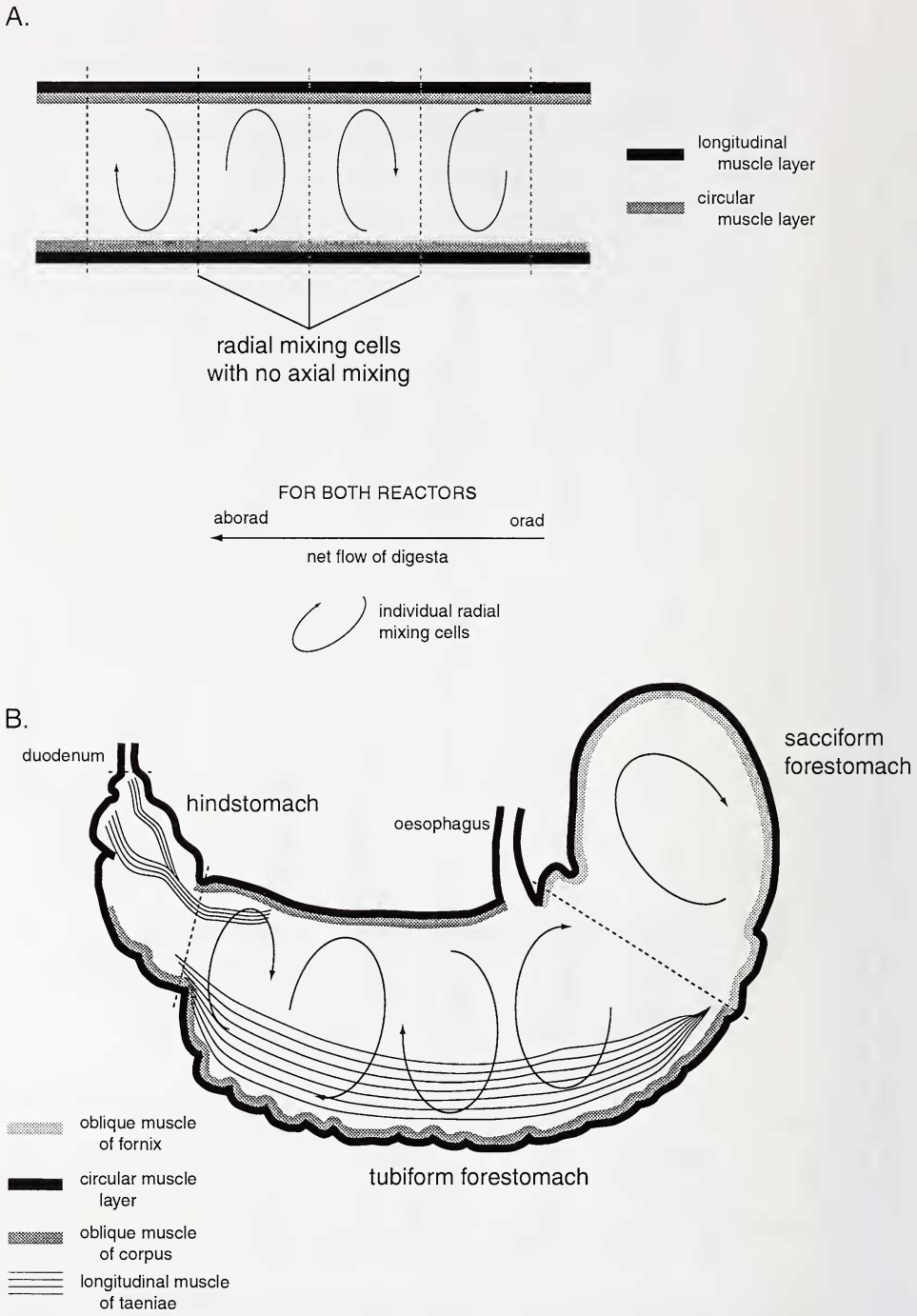

Fig. 3. Characteristics of plug-flow reactors of mammalian gastro-intestinal tracts. The small intestine (A) is a simple plug-flow reactor and its structure and function is constant throughout the phylum. The forestomachs of the herbivorous Macropodidae (kangaroos and wallabies) function as complex plug-flow reactors. (Drawing of the macropodid forestomach after LANGER 1988).

the caecum and colon is regulated by the caeco-colic sphincter, which is both the entry and the exit port (Tab. 3; Fig. 2 B). Taeniae and haustra, which facilitate mixing of the contents, are frequently present in these semi-batch reactors.

Gastro-intestinal plug-flow reactors are elongated tubular compartments that can be divided into two types, simple and complex, depending on their morphology and function (Tab. 1). The flow of reactants is unidirectional. Digesta are released into the plug-flow reactors in discrete batches through well-developed sphincters (Malagelada et al. 1984; Malagelada and Azpiroz 1989; Stevens and Hume 1995). The performance of the simple plug-flow reactor is closest to that of the ideal plug-flow reactor, differing from it in the continual absorption of digestion products and the motility of the wall (Weems 1987; Stevens and Hume 1995). The small intestine, which is the major site of catalysis in the mammalian gastro-intestinal tract, is a simple plug-flow reactor (Fig. 3 A). The tunica muscularis in the small intestines of all mammals consists of an outer longitudinal coat (adjacent to the serosa) with a circular coat inside that (Fig. 3 A).

Complex plug-flow reactors, or modified plug-flow reactors (Tab. 4), are adapted for fermentation through morphological changes, especially in the tunica muscularis (Fig. 3 B). These modifications result in longer retention times, increased axial mixing of the contents of the compartment and maintenance of suitable environmental conditions for cellulolytic micro-organisms (Dellow and Hume 1982; Dellow et al. 1983). The macropodid forestomach is an example of a complex plug-flow reactor (Stevens and Hume 1995; Caton 1997) (Fig. 3 B).

The most important diagnostic features of plug-flow reactors, whether simple or complex, are their length, radial mixing and the unidirectional flow of reactants (Tab. 4). Increasing the length of plug-flow reactors increases their operational efficiency, as well as providing a greater surface area for the absorption of nutrients (Denbigh and Turner 1971; Chivers and Hladik 1980).

Simple continuous-flow, stirred-tank reactors are rare in mammalian gastro-intestinal tracts. The best examples are sac-like simple unipartite stomachs (Fig. 4), and the sacciform forestomach of some mammalian herbivores (Langer 1988; Hume 1989) (Tab. 1).

The capacious proximal segment of the hindgut, which is modified for fermentation in herbivores and omnivores, is a complex continuous-flow, stirred-tank reactor (Caton 1997) (Fig. 4 A). Complex continuous-flow, stirred-tank reactors are tubular in shape, like complex plug-flow reactors, and are sites of fermentation. They are hybrid reactors that have characteristics of both ideal plug-flow reactors and continuous-flow, stirred-tank reactors (Tab. 4; Fig. 4 C). Enlargement of the reactor by increasing the calibre of a compartment and haustration of the wall by longitudinal muscle bands or taeniae increases the amount of radial mixing. Alternating bouts of peristalsis and antiperistalsis facilitate axial mixing. The determination of the functional category of a complex reactor depends on the pattern of flow of digesta (e. g. unidirectional in a complex plug-flow reactor) and the amount of axial mixing that occurs (e. g. limited in a complex plug-flow reactor) (Tab. 4; Figs. 3 and 4).

Retention mechanisms in gastro-intestinal reactors

Mechanisms that delay and alter the pattern of digesta flow through compartments are common in the gastro-intestinal tracts of mammals. Retention mechanisms are of three general types:

(1) Functional mechanisms that work throughout a specified compartment, e. g. alternating periods of peristalsis and antiperistalsis in the human colon (Christensen 1989) assist in mixing the contents and delay the emptying of this complex continuous-flow, stirred-tank reactor

(2) Sphincters within gastro-intestinal tract compartments regulate the volume and rate of

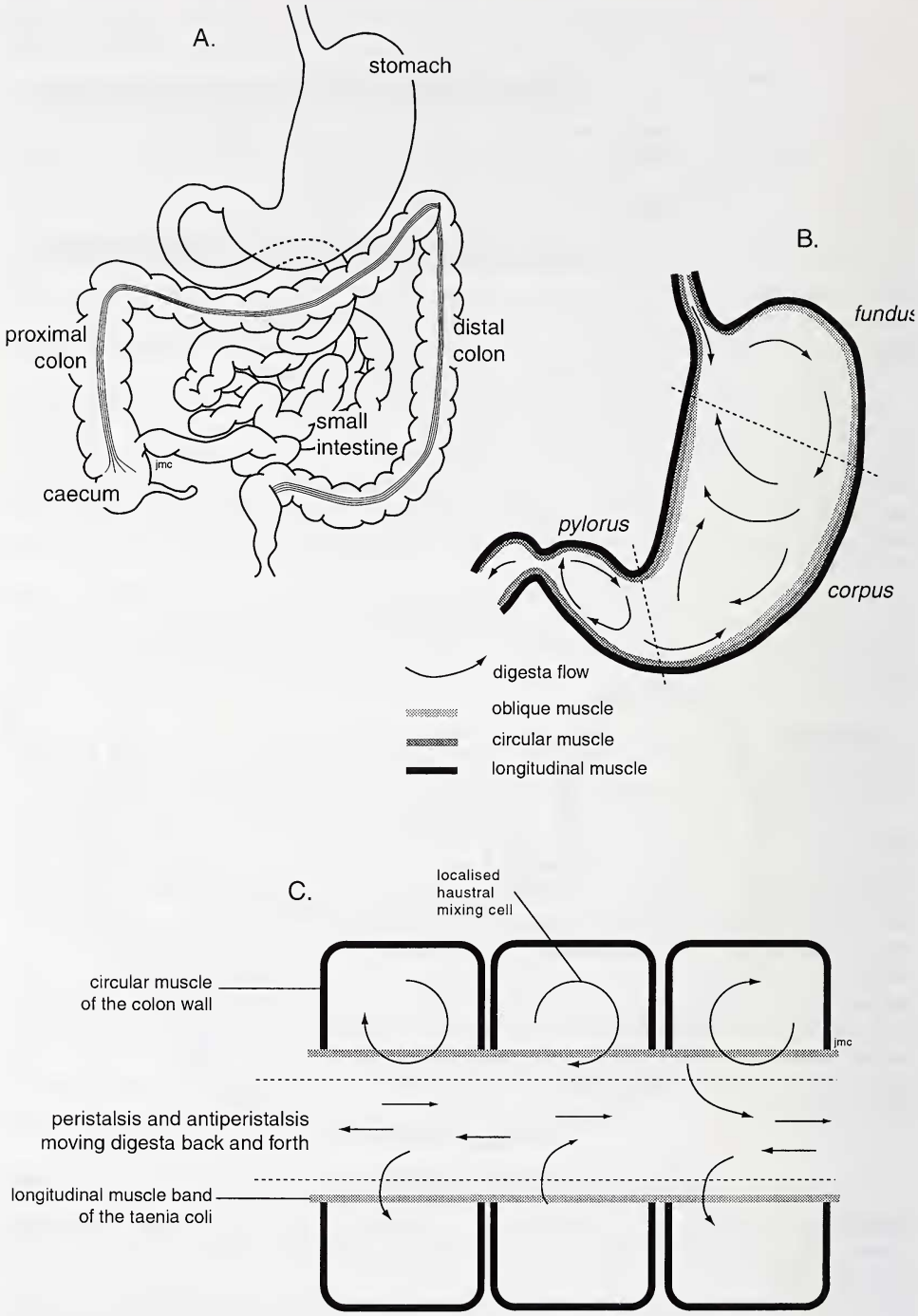

Fig. 4. Continuous-flow, stirred-tank reactors in the human gastro-intestinal tract (A). The Human stomach (B) functions as a simple continuous-flow, stirred-tank reactor for the preliminary processsing of digesta. The proximal colon and caecum (C) are a complex continuous-flow, stirred-tank reactor in which structural polysaccharides are processed by microbial fermentation.

aboral flow from one compartment to the next (Björnhag 1994; Stevens and Hume 1995). Sphincters also control the aboral flow of digesta through the gastro-intestinal tract (Papasova 1989).

(3) Specialised mophological features for directing digesta orally are evident in the hindguts of lagomorphs and certain rodents (Stevens and Hume 1995). Well-developed rugae (mucosal folds) are found in the stomachs of many mammals (Langer 1988; Stevens and Hume 1995; Caton 1997); these are 'baffles', increasing mixing of the contents of a compartment as well as delaying its transit.

These retention mechanisms are most often found in fermentation compartments. They improve the performance of continuous-flow, stirred-tank reactors by reducing by-pass loss and increasing retention times (thereby increasing the time available for the reaction to take place, which results in greater efficiency of fermentation compartments and increases the mixing capabilities of a particular compartment).

Conclusions

The application of chemical reactor theory to gut function has proved to be an important tool in the understanding of the complexity of the relationships between gut morphology, diet chemistry and food processing in the gastro-intestinal tract of mammals (Hume 1989; Caton 1997). The mathematical models developed have enabled physiologists to make detailed descriptions of the optimal reactor arrangements for processing specific diets, and thus to compare the digestive patterns of different species (Alexander 1991; Martinez Del Rio et al. 1994).

The widespread acceptance and use of chemical reactor theory in mammalian digestive physiology has necessitated the clarification and definition of the specific characteristics of gut reactors, which are the analogues of industrial reactors. The system of classification of mammalian gut reactors proposed here is based on both their structure and function (Caton 1997). Catalytic reactors, such as the human stomach and the small intestine, have simple morphologies. Fermentation compartments tend to have complex musculature, which facilitates the mixing and retention of digesta (Caton 1997). To avoid confusion with ideal reactors, gut reactors are defined as either simple or complex on the basis of their structure and functional characteristics.

The gastro-intestinal tract of mammals has the same basic morphology across taxa, despite phyletic and dietary differences (Stevens and Hume 1995). It is essentially a tubular structure that is divided into four compartments, stomach, small intestine, caecum and colon, each of which is adapted for either catalysis or fermentation (Chivers and Hladik 1980; Caton 1997). Ingesta are transported to the stomach via the oesophagus, where they are stored and prepared for sustained release into the tubular small intestine. The digesta then enter the hindgut, which consists of a blind diverticulum (the caecum) and tubular colon. Digestive wastes are voided into the environment via the anus. These morphologically distinct compartments perform different functions. The evolution of compartmentalisation of the mammalian tract separates catalytic and fermentation processes. This has resulted in greater flexibility in the processing of a range of dietary components and an increased ability to process larger amounts of ingesta per unit time. The importance of catalysis or fermentation in the digestive pattern of a particular species of mammal is reflected in the relative size of a compartment or reactor in which the processing of the significant dietary component occurs (Chivers and Hladik 1980; Stevens and Hume 1995; Caton 1997). The gastro-intestinal tract is more complex in plant-eaters as they rely to a much greater extent on fermentation than flesh-eaters (Stevens and Hume 1995).

The optimal reactor class for catalysis is the plug-flow reactor, if reaction rates are high (Denbigh and Turner 1971). The small intestine fits the criteria for this type of reactor (Tab. 3; Fig. 3), i. e. it is a long narrow tube; the concentration of reactants is highest

at the entrance to the reactor, where they are mixed with the catalysts (endogenous enzymes). There is limited axial mixing due to controlled segmental motility (peristalsis). The small intestine is always present in mammals irrespective of diet, but is relatively longer in mammals that eat high-quality diets (CHIVERS and HLADIK 1980).

Continuous-flow, stirred-tank reactors are the optimal reactor class for fermentation (DENBIGH and TURNER 1971). Characteristically, they have a vat-like structure with well-mixed contents and longer retention times to allow for slower reaction rates (Tab. 4; Fig. 4). Simple continuous-flow, stirred-tank reactors, which approach this ideal type, are found only in the stomach, either singly as in camivores and proximal hindgut fermenters, or in series as in the complex stomachs of herbivores (LANGER 1988). This arrangement of simple continuous-flow, stirred-tank reactors in series increases the efficiency of processing as it reduces by-pass loss (DENBIGH and TURNER 1971; ALEXANDER 1994). Ruminants, camelids, peccaries and sloths are the main groups exhibiting this type of gastric morphology (LANGER 1988; STEVENS and HUME 1995). The other two groups of forestomach fermenters, macropodids and colobines, have tubiform forestomachs. The macropodid forestomach functions as a modified plug-flow reactor (DELLOW 1979; HUME 1989) (Fig. 4). The function of the colobine stomach is more complex than that of macropodids, consisting of a continuous-flow, stirred-tank reactor in series with a plug-flow reactor (CATON 1997).

The morphology of the hindgut is modified in herbivores in which it is the major site of fermentation. The caecum acts either as a semi-batch reactor during fermentation (PENRY 1993), or as an extension of the colon (ELLIOTT and BARCLAY-SMITH 1904; BJÖRNHAG 1994). The tubular colon in these mammals is wide and haustrated for mixing and slowing the transit of contents (CHIVERS and HLADIK 1980; CLEMENS and PHILLIPS 1980; CATON 1997). Comparison of the characteristics of the functional morphology of the hindgut with those of ideal reactors is important in determining the types of reactors present in this region.

The differences in mammalian gut morphology and reactor classes represent adaptations to diets with different processing requirements (HUME 1989; ALEXANDER 1994). Strict herbivores and strict carnivores are dietary specialists representing the two ends of a dietary continuum. Omnivores, with their adaptations for processing mixed diets of variable chemical composition, have more flexible digestive abilities, enabling them to exploit a wide range of diets under variable environmental conditions.

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Zusammenfassung

Überblick über die Typen des Gastrointestinaltraktes von Säugetieren unter Berücksichtigung der „chemical reactor"-Theorie

PENRY und JUMARS (1986) nutzen als erste die Theorie der "chemical reactors" zur Modellierung der Wirkungsweise des Verdauungstraktes bei Säugetieren. Weil diese Theorie, in welcher der Verdauungsprozeß in Form eines mathematischen Modells dargestellt wird, es ermöglicht, die komplexen physiologischen Beziehungen zwischen Säugetier und seinem Futter besser zu verstehen, fand sie breite Zustimmung. Daten, welche im Rahmen physiologischer Untersuchungen an lebenden Säugern ermittelt wurden, können mit Hilfe der „chemical reactor"-Theorie das Verständnis der komplexen Beziehungen zwischen Morphologie, chemischer Zusammensetzung der Nahrung und Verdauungsprozessen bei Säugetieren erleichtern.

Im Verdauungstrakt der Säuger treten mehrere Reaktortypen auf. Gegenüber den „idealen" technischen Reaktionsgefäßen sind jene im Verdauungstrakt der Mammalia abgewandelt. Im Verdauungstrakt und im technischen System unterscheiden sich die Entfernung der Reaktionsprodukte aus dem Reaktor, aber auch die dort stattfindenden Mischungs- und Transportprozesse. Zur Vermeidung von Verwechslungen mit chemotechnischen Reaktortypen wird hier eine neue Klassifikation für die Reaktoren des Verdauungstraktes vorgeschlagen. Diese Klassifikation beruht auf Form- und Funktionsdifferenzen in den verschiedenen Abschnitten des Verdauungstraktes. Die im Gastrointestinaltrakt der Säugetiere auftretenden Reaktortypen ermöglichen die Anpassung an unterschiedliche Futterarten, welche unterschiedlichen Verdauungsprozessen unterworfen werden.

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